

Male–female evolutionary game on mate-locating behaviour and evolution of mating systems in insects

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Abstract

We present a model of a male–female evolutionary game on mate-locating behaviour. Two major mating systems are considered: “lek polygyny” (in which males aggregate to wait for females searching for males) and “searching polygyny” (in which males search for females emerging or waiting for males). The model predicts that lek polygyny is favoured (i) when male survivorship during lekking is sufficiently higher than that during mate searching, (ii) when female survivorship while visiting a lek is sufficiently higher than at the emergence site, or (iii) when searching efficiency is higher at a lek than at an emergence site. Furthermore, the model shows that a reduction in the reproductive value of females later in the day, which prevents males from performing riskier mate-locating behaviour, can result in a change of mating system. In addition, mixed mating systems can be realized as transient states during this shift.

Keywords

Lek polygyny, male–female game, mating system, mixed mating system, residual reproductive value, searching efficiency, searching polygyny.

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INTRODUCTION

The diverse mating systems observed in insect species have been classified into two common types: lek polygyny and searching polygyny (Wickman & Rutowski 1999). In lek polygyny, males aggregate at particular sites, often landmarks, to await females, while females move to the lek site to mate. On the other hand, in searching polygyny, males wander widely to search for females that are emerging or waiting for males. Commonly, the term “lek polygyny” is used *sensu stricto* for the case in which males cluster to mate, for instance on a landmark site. In this paper, however, we take lek polygyny in the broad sense that includes the mating systems with sit-and-wait strategy for males, following Wickman & Rutowski (1999).

Many studies on mate-locating behaviour have been carried out in various taxa, including lepidopterans (e.g. Dennis & Shreeve 1988; Rutowski 1991), dipterans (Kaspi & Yuval 1999), odonates (e.g. Nomakuchi 1992; Jennions 1998) and others (Choe & Crespi 1997). In these studies, many hypotheses were proposed to explain the conditions favouring lek polygyny or searching polygyny. Some authors focus on the male’s interests. They suggest that lek polygyny is preferred if the energetic cost of searching is high for inefficient flight

(Scott 1974) or wide dispersion and location unpredictability of females (Sivinski & Petersson 1997), or if mate availability is high near a certain spot (the hotspot model; Bradbury & Gibson 1983; Cordero & Soberón 1990) or a preferred male (the hotshot model; Beehler & Foster 1988). Other authors focus on the female’s interests. They suggest that lek polygyny is preferred if females simply prefer clustered males (the female-preference model; Bradbury 1981; Hibino 1986) or if females move relatively long distances (Wickman & Rutowski 1999) or if females are more selective because they have a longer selecting time as a result of their longer lives (Thornhill & Alcock 1983).

However, there are problems with these hypotheses. They consider the interest of one sex alone, whereas in reality the different interests of both sexes are thought to determine the mating system. Moreover, a game theoretical situation involving mate numbers has been ignored. Males moving to emergence sites would be favoured by selection if more females stay there, whereas males joining a lek would be favoured if most females visit the lek. Similarly, a female visiting a lek would be favoured if most males engage in lekking, whereas a female staying at the emergence site would be favoured if males do not form a lek and search for emergence sites. Furthermore, these hypotheses fail to explain why both mating systems

occur in some populations (Sims 1979; Ehrlich & Wheye 1986; Wolf & Waltz 1993) or why the mating system switches from one to the other according to temperature (Wickman 1985, 1988; Alcock 1994) or time (Kon *et al.* 1986; Dennis & Williams 1987; Watanabe 1998) within a day. Courtney & Parker (1985) presented a model to explain the case where both mating systems occurred in one population. In this model, however, the lek was assumed to be formed at oviposition sites, and only the male's interest was considered.

Here we present a model that provides a theoretical framework for understanding mating-system evolution in insects. The key is to consider the interests of both sexes and the male–female coevolutionary game on mate-locating behaviour. This model makes testable predictions which relate diverse mating systems to several environmental constraints. Additionally, a hypothesis is presented to explain the change in mating system with time.

THE BASIC MODEL

Consider a population of an insect species composed of M sexually active males and F receptive females. Suppose that all the females are at an emergence site, whereas the males are dispersed over space. An individual of each sex chooses a mate-locating behaviour from two alternatives. Males can choose lekking or searching for an emergence site; females can visit a lek or stay at the emergence site (Fig. 1). Then male–female encounters can occur at a lek site between lek-forming males and lek-visiting females, or at an emergence site between searching males and staying females.

We assume that a male and a female adopt the dispersing strategy with probability, p and q , respectively. (The alternative assumption that pM males and qF females adopt the dispersing strategy does not alter the model or its results.) Suppose that most males and females adopt the same strategy, p^* and q^* , respectively. The expected number of mates for a mutant male and a mutant female with slightly different strategy, p' and q' , is given by

$$N_m = p' b_m \frac{e_s a_f (1 - q^*) F}{b_m p^* M} + (1 - p') a_m \frac{e_l b_f q^* F}{a_m (1 - p^*) M} \quad (1a)$$

and

$$N_f = q' b_f \frac{e_l a_m (1 - p^*) M}{b_f q^* F} + (1 - q') a_f \frac{e_s b_m p^* M}{a_f (1 - q^*) F}, \quad (1b)$$

respectively, where a_m and b_m are the survivorship of lekking and searching males; a_f and b_f are the survivorship of waiting and lek-visiting females; e_l and e_s (≤ 1)

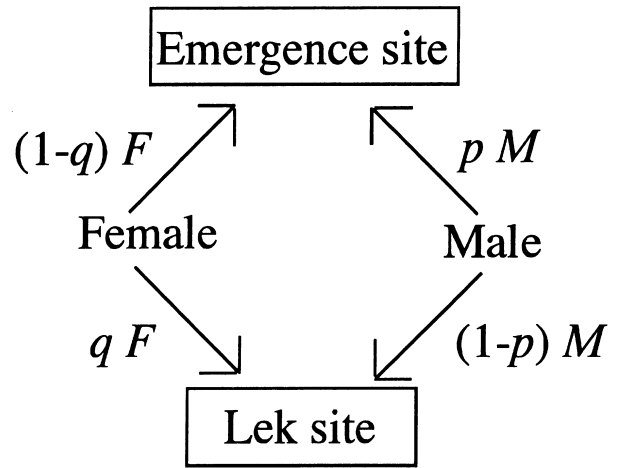


Figure 1 The mating systems considered in the model. The population consists of M males and F females. p^*M males and $(1 - q^*)F$ females engage in mating at an emergence site, whereas $(1 - p^*)M$ males and q^*F females engage in mating at a lek site.

represent searching efficiency at a lek site and an emergence site. The fitness of the mutant males and females is given by

$$W_m = w_m(N_m) \quad (2a)$$

and

$$W_f = w_f(N_f), \quad (2b)$$

respectively, where $w_m(N)$ and $w_f(N)$ represent the fitness gain as increasing functions of the number of mates located by a male and a female, respectively. For polygamous males, whose reproductive success is limited by the number of mates, reproductive success is thought to increase with the number of available mates (Bateman 1948; Trivers 1972; Thornhill & Alcock 1983). Even for monogamous males or females, a larger number of mates can be beneficial. Because it increases the opportunity to perform mate choice to mate with a high-quality mate (Thornhill & Alcock 1983) or because it decreases the searching time so that it increases the period spent on oviposition (Wickman & Jansson 1997). For simplicity, in this paper, we assumed that the fitness of each sex, w_m and w_f , is an increasing function of the respective number of mates, N_m and N_f .

Assume that the strategies of the sexes are concentrated around the population average, p^* or q^* . When the fitness of a mutant with a slightly different strategy, p' or q' , is larger than that of a wild type, p^* or q^* , the mutant invades the population, and the average phenotype shifts toward that of the mutant.

Evolutionary equilibrium is obtained by a vector field of (p^*, q^*) , where the zero isoclines for p^* and q^* are given as $\partial W_m / \partial p' |_{p'=p^*} = 0$ and $\partial W_f / \partial q' |_{q'=q^*} = 0$ (Fig. 2).

There are only two possible evolutionary equilibria. If the survivorship of mate-searching males (b_m) is sufficiently higher than the survivorship of lekking males (a_m), if the survivorship of females staying at an emergence site (a_f) is sufficiently higher than the survivorship of females visiting lek sites (b_f) or if the searching efficiency at an emergence site (e_s) is sufficiently higher than the searching efficiency at a lek site (e_l) (to hold that $a_f b_m / b_f a_m > (e_l / e_s)^2$), at the evolutionary equilibrium (which is continuous stable: CS; Christiansen 1991), all females stay at the emergence site and all males search for females, i.e. $(p^c, q^c) = (1, 0)$ (Fig. 2a). In contrast, if the survivorship of mate-searching males (b_m) is sufficiently lower than the survivorship of lekking males (a_m), if the survivorship of females staying at an emergence site (a_f) is sufficiently lower than the survivorship of females visiting lek sites (b_f) or if the searching efficiency at a lek site (e_l) is sufficiently higher than the searching efficiency at an emergence site (e_s) (to hold that $a_f b_m / b_f a_m < (e_l / e_s)^2$), this system converges on another equilibrium in which all females visit a lek and all males form a lek, i.e. $(p^c, q^c) = (0, 1)$ (Fig. 2b). These results imply that at equilibrium, all matings occur at either a lek site or an emergence site, and no mixed mating system can be realized.

THE EXTENDED MODEL

In the last section, we considered the simplest case, where the reproductive success of the sexes is determined only by present matings. In some species, however, a mating period for males is much longer than that of females (Ohtani & Yamamoto 1985; Suzuki & Matsumoto 1992) and males that die during a reproductive event may suffer the large cost of failing to ensure future reproductive events. In this section, we consider the case in which males experience multiple reproductive events.

The fitness of mutant males adopting the strategy p' is given by

$$W_m = u_m(N_m) + \{(1 - p')a_m + p'b_m\}S \tag{3a}$$

where S is the value of the expected future reproduction, and $\{(1 - p') a_m + p' b_m\}$ is the probability that the male survives the present reproductive event. The second term implies that males that do not survive the present bout of reproduction lose all future reproduction. Note that S is determined by both the number of future reproductive events and the future sex ratio; it is lower when a male is old or when the future sex ratio is biased towards males. For simplicity, we assume that k (N

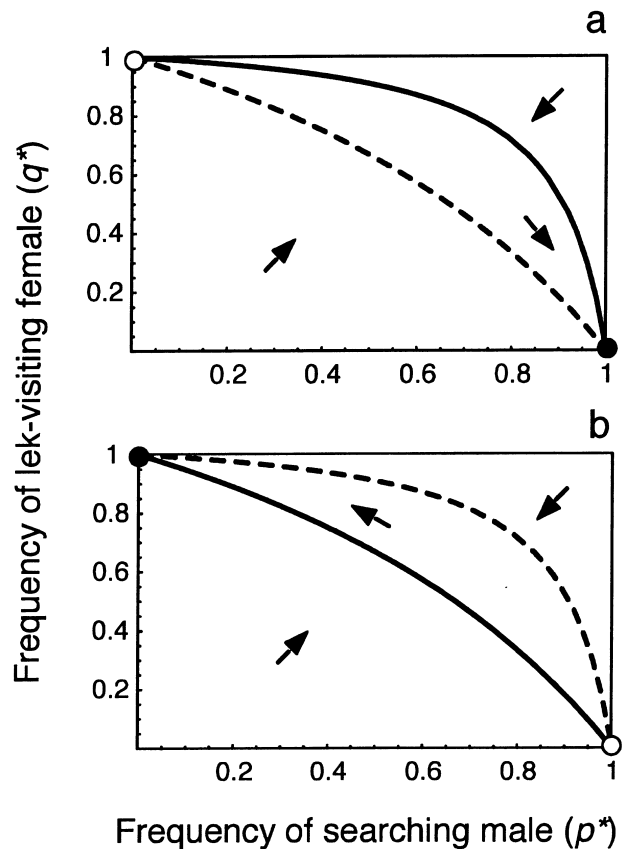


Figure 2 A typical vector field used for the coevolutionary dynamics of searching males and lek-visiting females (p^* and q^* , respectively) in the basic model (i.e. $S = 0$). Solid and broken lines represent the zero-isoclines for the dynamics of p^* and q^* , respectively. The parameters $(e_l, e_s, a_m, b_m, a_f, b_f) = (1, 1, 1, 0.5, 1, 0.1)$ for (a) and $(e_l, e_s, a_m, b_m, a_f, b_f) = (1, 1, 1, 0.1, 1, 0.5)$ for (b). In (a), the system converges to an equilibrium at which all individuals mate at an emergence site. In (b), the system converges to an equilibrium at which all individuals mate at a lek site.

$k) = \phi_k N_k$ (where $k = m$ or f), where ϕ_m is assigned a lower value when the current female mate has fewer eggs to be fertilized.

By using equations (2b) and (3a), the coevolutionary equilibria for this extended model are obtained. As in the basic model, the coevolutionary dynamics are given by a vector field, as shown in Figs 3 or 4.

The model analysis suggests that a larger S favours the system with the higher male survivorship (i.e. lek polyandry if $a_m > b_m$, searching polyandry if $a_m < b_m$). Therefore, S has no effect on the equilibrium mating system when the system favoured when $S = 0$ is less risky for males (i.e. $a_f b_m / b_f a_m > (e_l / e_s)^2$ and $a_m < b_m$; or $a_f b_m / b_f a_m < (e_l / e_s)^2$ and $a_m > b_m$). However, a different picture emerges when the system with the higher risk for males is favoured when $S = 0$ (i.e. $a_f b_m / b_f a_m > (e_l / e_s)^2$ and a_m

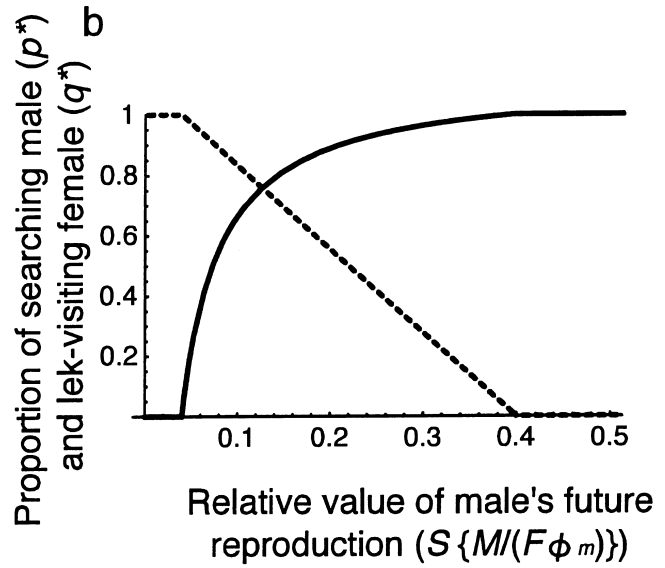
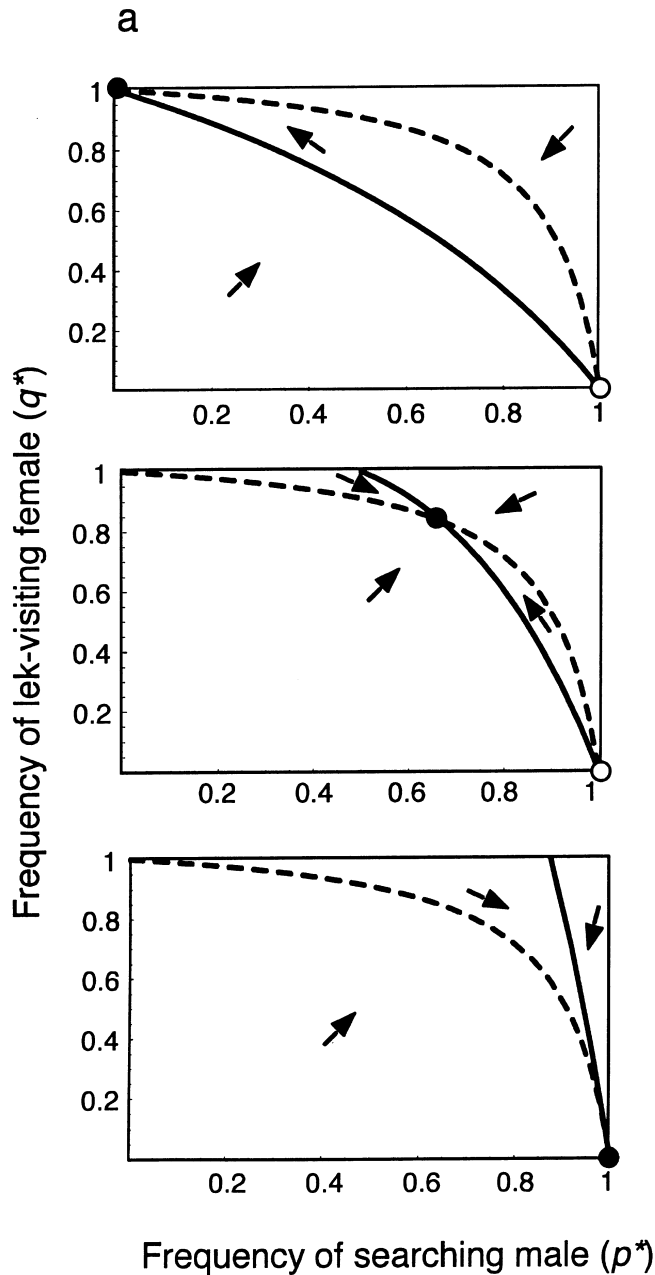


Figure 3 The effect of the relative value of future reproduction to the present reproduction, $S\{M/(F\phi_m)\}$ on the coevolutionary dynamics and the equilibrium mating system for the case in which a mixed mating system can be realized. (a) Examples of a vector field for the coevolutionary dynamics of the frequency of searching male and lek-visiting female (p^* and q^* , respectively) for different $S\{M/(F\phi_m)\}$. The solid and broken lines represent the zero-isoclines for the dynamics of p^* and q^* , respectively. The values of $S\{M/(F\phi_m)\}$ used in this panel are 0 (top), 0.1 (centre) and 0.4 (bottom). The other parameters are $(e_i, e_s, a_m, b_m, a_f, b_f) = (1, 0.05, 0.5, 1, 1, 0.025)$. (b) The equilibrium proportion of searching males (p^*) and lek-visiting females (q^*) against $S\{M/(F\phi_m)\}$.

$> b_m$; or $a_f b_m / b_f a_m < (e_i / e_s)^2$ and $a_m < b_m$). In this case, the system with the higher male risk (i.e. the system that is very safe for females or has the higher searching efficiency) is favoured when the male's future reproduction is low, whereas the system with the lower male risk (which is very risky for females or has the lower searching efficiency) is favoured when the male's future reproduction is high (Figs 3a and 4a).

Furthermore, this model can generate a mixed mating system. Suppose that the system with the higher risk for males, lek polygyny (case i) or searching polygyny (case ii), is favoured when $S = 0$ (i.e. $a_f b_m / b_f a_m < (e_i / e_s)^2$ and a_m

$< b_m$ for case i, or $a_f b_m / b_f a_m > (e_i / e_s)^2$ and $a_m > b_m$ for case ii). Under these conditions, if the searching efficiency at the lek site (case i) or emergence site (case ii) is sufficiently higher than the searching efficiency at the other site (to hold that $e_s b_m < e_i a_m$ for case i or that $e_s b_m > e_i a_m$ for case ii), a mixed mating system of searching and lek polygyny is realized, where

$$p^* = e \frac{a_m b_f - e_s^2 a_f b_m - S(M/F\phi_m) a_m e_i (b_m - a_m)}{S(M/F\phi_m) (b_m - a_m) (e_s b_m - e_i a_m)} \tag{4a}$$

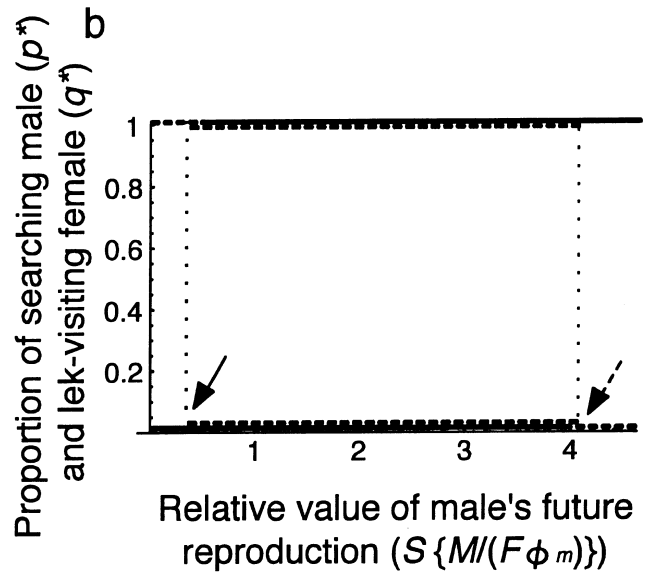
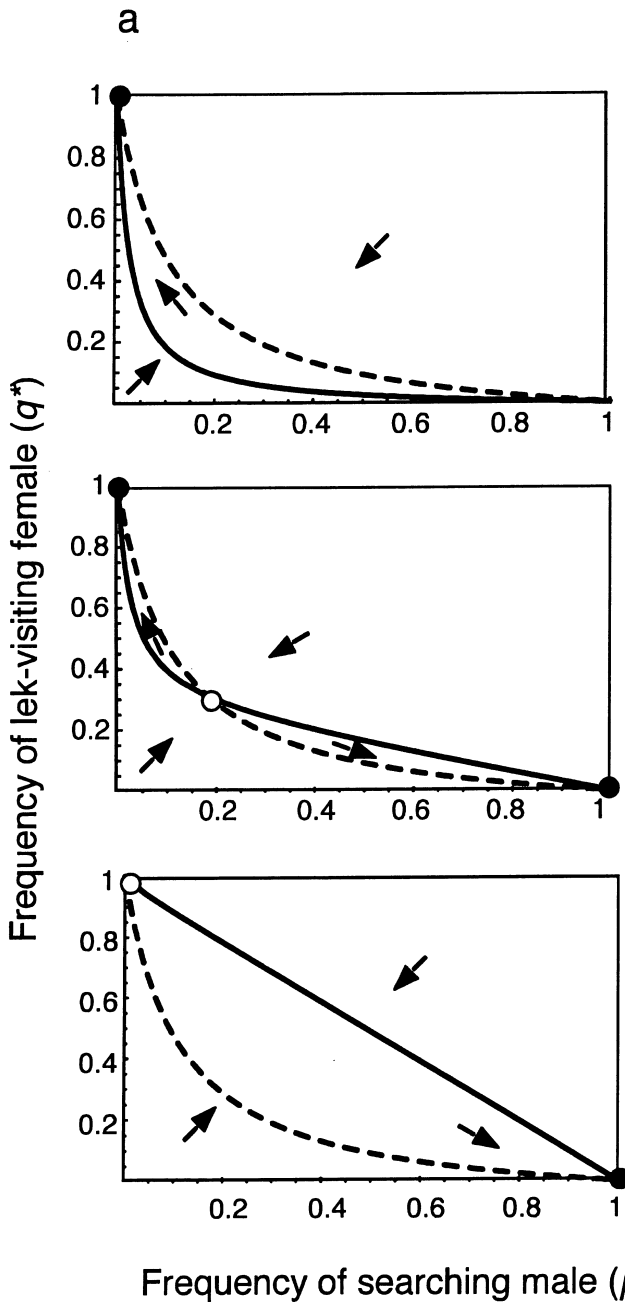


Figure 4 The effect of the relative value of future reproduction to the present reproduction, $S\{M/(F\phi_m)\}$, on the coevolutionary dynamics and the equilibrium mating system for the case in which a mixed mating system can never be realized. (a) Examples of a vector field for the coevolutionary dynamics of p^* and q^* for different $S\{M/(F\phi_m)\}$. The solid and broken lines represent the zero-isoclines for the dynamics of p^* and q^* , respectively. The values of $S\{M/(F\phi_m)\}$ used in this panel are 0 (top), 1.5 (centre) and 5 (bottom). The other parameters are $(a_i, e_s, a_m, b_m, a_f, b_f) = (1, 0.5, 0.01, 0.2, 0.05, 1)$. (b) The equilibrium frequency of mating at emergence sites and lek sites against $S\{M/(F\phi_m)\}$. The switch between mating systems occurs at the point indicated by an arrow with a solid line when $S\{M/(F\phi_m)\}$ gradually decreases, whereas it occurs at the point indicated by an arrow with a dashed line when $S\{M/(F\phi_m)\}$ increases.

and

$$q^* = \left\{ \frac{1}{(e_s b_m / e_f a_m) - 1} \right\} \left\{ \frac{S(M/F\phi_m)(b_m - a_m)e_s b_m}{e_f^2 a_m b_f - e_s^2 a_f b_m} - 1 \right\} \quad (4b)$$

(derived as the intersection of the zero-isoclines for p^* and q^*) when the relative value of the male's future

reproduction to its present reproduction, $S\{M/(F\phi_m)\}$, is intermediate (i.e. $\{1/(b_m - a_m)\}\{e_f^2 a_m b_f / e_s b_m\} - e_s a_f\} < S\{M/(F\phi_m)\} < \{1/(b_m - a_m)\}\{e_f b_f - (e_s^2 a_f b_m / e_f a_m)\}$) (Fig. 3b). In contrast, if the searching efficiency at the lek site (case i) or emergence site (case ii) is sufficiently lower than the searching efficiency at the other site (to hold that $e_s b_m > e_f a_m$ for case i or that $e_s b_m < e_f a_m$ for case ii), a mixed system can never be realized, but two stable points (1, 0) and (0, 1), exist when the relative value of the male's future reproduction to its present reproduction,

$S\{M/(F\phi_m)\}$, is intermediate (i.e. $\{1/(b_m - a_m)\}\{e_1^2 a_m b_f / e_s b_m\} - e_s a_f < S\{M/(F\phi_m)\} < \{1/(b_m - a_m)\}\{e_1 b_f - (e_s^2 a_f b_m / e_1 a_m)\}$) (Fig. 4b).

DISCUSSION

In this paper, we show how an evolutionary game involving the mate locating strategies of males and females shapes a mating system. It can generate diverse mating systems, including lek polygyny, searching polygyny or a mixed system. The result can be summarized as follows. With this model, the mating systems are related to environmental conditions. The basic model predicts the environmental conditions that favour lek polygyny (or searching polygyny); (i) male survivorship while searching for mates is sufficiently lower (or higher) than male survivorship during lekking, (ii) female survivorship while visiting a lek is sufficiently higher (or lower) than female survivorship staying at an emergence site, and (iii) the searching efficiency is sufficiently higher (or lower) at a lek than an emergence site. The model suggests that the mating system with higher male survivorship is favoured with increasing future reproduction or decreasing present reproduction for males. Furthermore, this is due to the change in the relative value of present mating to future mating.

These results suggest that environmental constraints that alter the cost or efficiency of searching, lekking, lek-visiting or waiting behaviour have the potential to alter the mating system. One good example is temperature, which constrains the activity of insects. Males of the inornate ringlet butterfly, *Coenonympha inornata*, use a searching strategy for mate-locating only when the air temperature is high (Heinrich 1986). This temperature-dependent change in male behaviour may cause a change in the mating system as observed in some butterfly species (Wickman 1985, 1988; Alcock 1994). The location of a lek site or an emergence site is also thought to play an important role in shaping the mating system for two reasons. First, the survivorship of the sexes adopting each strategy depends on the location of the mating site. For example, lek polygyny is predicted to be favoured when the survivorship of both sexes is high at a lek site because of reduced predation pressure (Karban 1982; Hendrichs & Hendrichs 1990). Second, searching efficiency also depends on the mating-site location. If the distribution of mates is unpredictable and if a lek site is a distinctive landmark, a lek site is so much easier to find that lek polygyny would be favoured (Dennis & Shreeve 1988).

The change of the mating system within a day can be explained by the change in the relative value of a mating within a day. Suppose that there is a population with a

mating system with higher male mortality. If females eclose synchronously in the early morning and their fecundity decreases by delaying copulation, as is thought to occur widely in short-lived insects (e.g. Wickman & Jansson 1997), males may not produce many offspring by mating with females in the afternoon. Then it follows that, in the afternoon, survivorship is more important than copulating with such a female, and the mating system with the lower male mortality becomes more common. This explains the shift of mating system from searching polygyny to lek polygyny, or vice versa, which is observed in some insect species (Kon *et al.* 1986; Dennis & Williams 1987; Watanabe 1998). By contrast, when fecundity does not decrease with delayed copulation (e.g. Hiroki & Obara 1997), a switch of mating system does not occur, supporting our model. A decreased number of receptive females towards the afternoon (Dennis & Williams 1987), which reduces the value of present reproduction, can also shift the mating system.

A shift of mating system can also be caused by an increased number of mates already accepted by a female, when later males are less likely to fertilize the eggs. The chironomid midge, *Tokunagayusurika akamusi*, ecloses synchronously in the early morning. Males mate primarily with fresh females soon after eclosion because fresh females are more likely to have eggs that the male can fertilize (Otsuka *et al.* 1986). This leads to a reduction in the value of a female with time. The switch of mating system from searching to swarming (lekking) with time of day in this species (Kon *et al.* 1986) may be caused by this mechanism.

A mixed mating system of lek polygyny and searching polygyny is observed in some insect species (Sims 1979; Ehrlich & Wheye 1986; Wolf & Waltz 1993). However, few hypotheses explain how such a mixed system can evolve, except for the species with intrasexual dimorphism (Shreeve 1987; Van Dyck *et al.* 1997a, b; Van Dyck & Matthysen 1998) or remarkable individual differences (Hernández & Benson 1998; Takamura 1999). It is notable that in the extended model, male–female coevolution of mate-locating behaviour can generate the mixed mating system as a transient state between pure lek polygyny and pure searching polygyny. The model predicts that such a mixed-system evolves under the following conditions. (i) The mating system in which it is more efficient to search for mates or is much less risky for females is riskier for males than the other mating system, and (ii) the male's potential for future reproduction is intermediate or present female's clutch size is intermediate.

In this model, population density never alters the realized mating system. However, this result is due to some simple assumptions of the model. Low population density is thought to be one of the major factors in the

evolution of lek polygyny (Scott 1974; Lederhouse 1982; Ehrlich & Wheye 1986; Kon 1987; Baughman *et al.* 1988; Suzuki 1988; Wickman & Rutowski 1999), because these authors believed that the lower the population density, the heavier the travelling cost for searching. This nonlinear relationship of population density and searching efficiency may result in density-dependent mating systems. Another possible mechanism for the effect of density on mating systems is that at a low population density, the variance of mating success between individuals is larger, and the probability that an individual cannot mate is also larger. So a low population density may favour a mating system that is more certain or has a smaller variance as a risk-averse behaviour (see Caraco 1981). However, it is unclear which mating system is favoured by a lower population density, because there is no way to say which mating system generally shows a smaller variance in mating success (Nishida 1992).

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